NON-CRISS-CROSS INHERITANCE IN DROSOPHILA MELANOGASTER.

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A complete reversal of the ordinary criss-cross inheritance of recessive sex-linked characters occurs in a line of *Drosophila* recently obtained. In ordinary sex-linked inheritance the recessive sex-linked characters of the mother are transmitted to the sons, while the daughters show the dominating allelomorphic characters of the father. In the present case the daughters show a recessive sex-linked character of the mother and the sons show the dominating allelomorphic character of the father. The reversal is explicable on the assumption that the two X-chromosomes of the mother are united and behave at reduction as a single body. Sections show that the eggs of these females do have two united X-chromosomes; the cytological evidence verifies the genetic deduction.

A female fly (Fig. 1, *a*), which was a somatic mosaic, showing different sex-linked characters in the anterior and posterior parts, appeared in a pair culture of which the parents had the following constitution: one X of the mother carried the differentials for eosin, cut and forked; the other X carried the differentials for forked and bar. She was therefore forked, heterozygous bar, and gray. The X of the father carried the differential for yellow body color, and he was therefore yellow.

The head and thorax of the mosaic (Fig. 1) were gray and the eyes were slightly bar, while the abdomen was yellow; the fly was entirely female, having heterozygous bar eyes, no sex-combs, and normal female genitalia. She was not virgin, but nevertheless was isolated and mated to a black male, and produced 43 daughters and 59 sons. The daughters were, without exception, all yellow and the sons were all gray, and all the offspring had wild type eyes—*i.e.*, none were bar except two sons that were also forked and will be considered later. The conclusion was at once evident that the mosaic fly had received from its father two yellow-bearing chromosomes, inseparable from one another, and that these inseparable

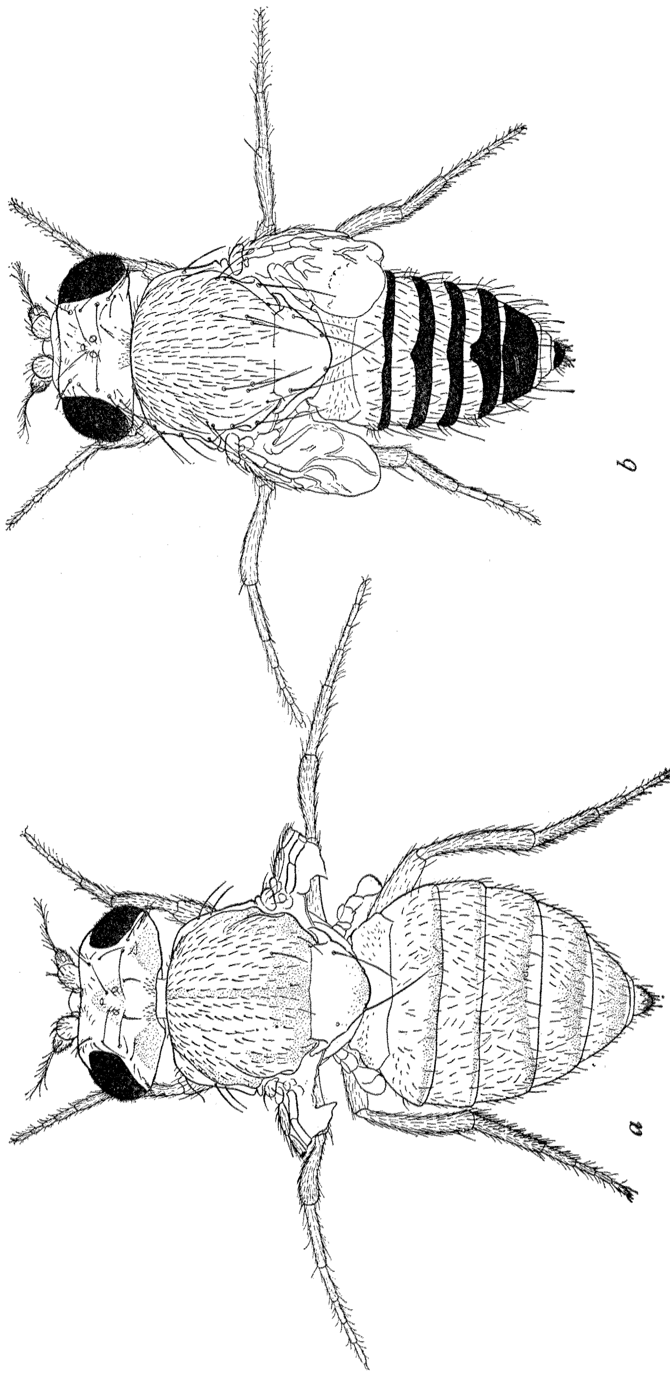

FIG. 1. *a*, Mosaic female fly (wings cut off); head, thorax (grey wings) and legs, wild type color (heterozygous for black); eyes slightly Bar; balancers and abdomen yellow (with light bands of yellow type). *b*, Triploid-X female, "grey" with abnormal wings, and flat, small abdomen.

chromosomes were transmitted together to the next generation, producing (wherever they occurred) females, because there were always two of them. No male offspring could be yellow, because no single yellow chromosome was transmitted (see Fig. 2). The sons must receive their X-chromosome from their father. The mosaic, as already stated, was not virgin; her brothers were all forked and some of them were bar, so that the two forked bar sons were in all probability offspring of a first mating and the other sons were offspring of the black male.

Three of the F_1 females were mated to three brothers, but no one of the pairs produced offspring; neither did a mass culture of F_1 males and females, nor did three F_1 males outcrossed to yellow-white females have any offspring. On the other hand, F_1 females outbred were fertile, and the sons of these were also fertile. The sterility of the F_1 males was expected if the X-chromosomes of the mosaic parent remained together, as the analysis shows, for then she should have produced two kinds of eggs (cf. Fig. 2), one kind with the double X and one kind with no X-chromosome. The XX-eggs fertilized by X-sperm would have produced XX X females (triploid-X females which would die); the XX-eggs, fertilized by Y-sperm, would have produced XXY females, the yellow daughters. The no-X or O-eggs, if fertilized by X-sperm, would have produced XO males, in appearance like the father, but sterile because lacking a Y-chromosome, and the O-eggs fertilized by Y-sperm would have produced YO males which would have died. Half the F_1 males and half the F_1 females presumably died and the sex-ratio remained 1 : 1. The actual numbers were 43 females to 59 males. The daughters were all yellow, but differed from their yellow mother in having, besides the "yellow-bearing" double chromosome, a Y-chromosome from their father; their sons therefore received from them a Y-chromosome and were fertile, and the surviving half, receiving their X-chromosome from the father, resembled him. Such patroclinous sons were produced by mating F_1 yellow daughters to wild type, to yellow white, to Xple, and to yellow broad, eosin, ruby males. The ratio of females to males in 8 cultures was 435 : 437, as would be expected again in this generation, since out of the four classes one class of females (XX X) would die, one class (XX Y) would survive, one class of

males (XY) would survive, and one class (YY) die (Fig. 2). In subsequent generations the line of double yellow females has remained intact; crosses have been made to many more types of males, always producing males like the father. The double yellow females are now used when it is desired to keep a supply of a certain type of male, for, since the X-chromosomes are inseparable, any egg which receives them produces a female, and only those eggs which receive the father's X can produce males. In such a line, then, there is never any crossing over in the X-chromosomes, and any desired combination of sex-linked characters can be maintained in the male flies by mating a male having the characters to a double yellow female. This is useful in cases where females of the race are weak or sterile, or where the pure cultures of the desired characters are weak, as frequently happens with a complicated combination of characters. The double yellow females are very vigorous and afford a reliable medium upon which to rear a race of feeble males. A possibility of a break in the continuity of a pure culture, which is easily discovered and rectified, will be discussed later.

The double yellow females probably behave like other flies in regard to the inheritance of characters in the autosomes. The original mosaic was dichete and transmitted the character normally. Crossing over in the second chromosome was tested by mating double yellow females to black purple vestigial lobe males and was found to be normal. Crossing over in the third chromosome was tested by mating double yellow females to pink, spineless, kidney, sooty, rough males, and found to be normal at the left end of the chromosome, but not at the right end; the discrepancy may, however, be due to the difficulty in classifying sooty in the presence of yellow.

X-Triploids.

After many hundreds of flies had been examined, there appeared occasionally, in cultures where the males were gray, wild type females of a more or less abnormal appearance; the eyes were somewhat rough and smaller than normal, the wings more or less imperfect and sometimes serrated, the abdomen imperfect, and the flies were weak (Fig. 1, *b*). These are characteristics of females

triploid for X. It is clear that from time to time a three X female survives. She has gray wings and body color like the father, because two yellow genes are recessive to one wild type gene. In a culture where the father was bar, the X-triploids had eyes less bar than in a heterozygous female, yet showing the character bar; this is known to be the appearance of bar when carried in one chromosome in the presence of two other chromosomes, both carrying the gene for wild type. X-triploids have not been observed in all of the cultures, and the percentage of them when present varies very much. In one culture their number was for a time about equal to the number of yellow females. All of many attempts to breed them have failed.

Occasional Breaking Apart of the Double Chromosome.

No exception to the non-criss-cross inheritance was observed until the F_4 generation, when a single yellow male appeared in a line in which all the other males were wild type. The yellow chromosomes of the mother had in this case presumably broken apart and the usual type of sex-linked inheritance from mother to son had been restored. The fly bred like an ordinary yellow male. At about the same time, in each of two related cultures of double yellow females by cross-veinless, cut, forked males, there appeared a wild type female not having the characteristics of an X-triploid. Both of these flies were fertile and both bred like females having one yellow-bearing X-chromosome, and one X-chromosome bearing the characters of the males of the cultures—*i.e.*, having the differentials for cross-veinless, cut and forked. One of these females was bred to a brother and produced females of two classes (wild type and cross-veinless, cut, forked) and yellow sons, and cross-veinless, cut, forked sons and the cross-over classes to be expected. The other wild type female was bred to a 7ple male and also produced yellow sons and cross-veinless, cut, forked sons, and females and cross-overs of the classes to be expected. These two females, like the yellow male of the other culture, had received from the mother a single yellow chromosome, broken apart from its mate. Since these flies occurred there have appeared in cultures of double yellow females six other yellow males and two wild type, not X-triploid, females. All the males have been bred and all but one

have produced offspring of the expected classes. Another female of the same kind undoubtedly occurred in a mass culture of double yellow females, for there were found in the culture some yellow

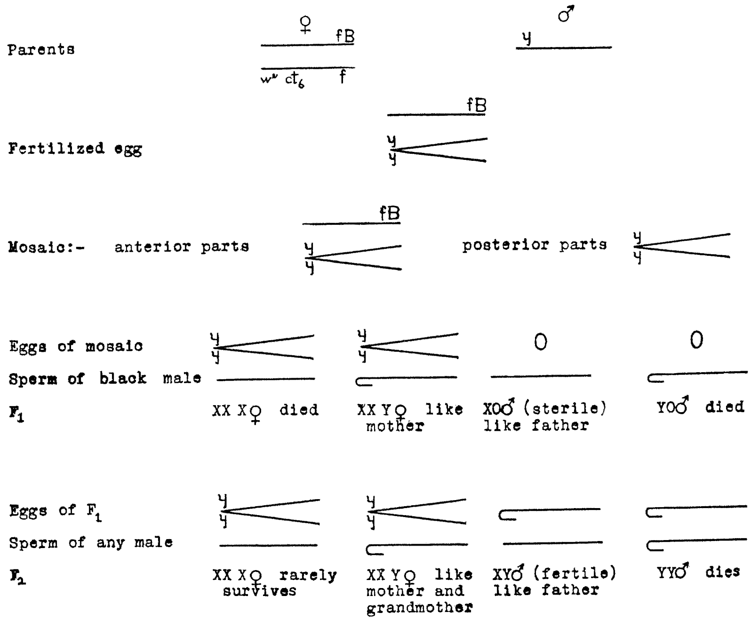

FIG. 2. Diagram showing parentage and constitution of the mosaic and of the line of non-criss-cross inheritance. The components of the double chromosome are arbitrarily represented as attached at "left" end.

males and cross-over males and females of classes to be expected if a female heterozygous for yellow had been present in the culture.

The question as to whether the break occurs in the place of the original attachment of the chromosomes has not been fully tested, but so far there is no evidence of duplication or deficiency at either end of the detached chromosome.

CYTOLOGY.

The genetic behavior of the line of flies having the two inseparable sex-chromosomes is in entire accord with the condition of the chromosomes as seen in cytological preparations of yellow females and of their rare wild type XX X sisters. Both of these classes of females receive from the mother not a single X, but two

X's attached to one another; the yellow female should have, in addition, a Y-chromosome from her father (Fig. 2, last line), the wild type female an additional X-chromosome from her father. Such chromosomes are, in fact, found in the maturation stages of the eggs of these females (Fig. 3, *b, c, d* and *e, f, g, h*). In both

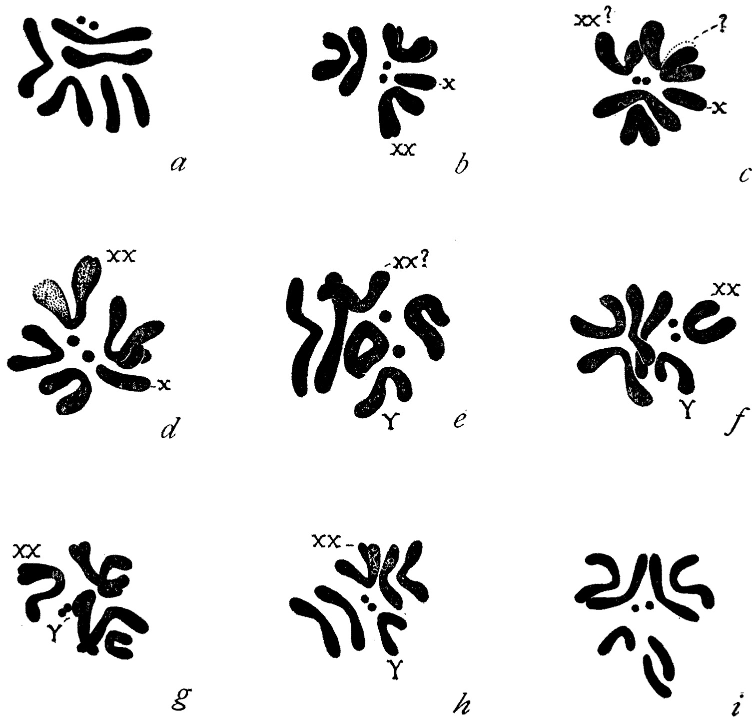

FIG. 3. Oögonial plates of: *a*, wild type female (after Bridges); *b, c, d*, triploid-X grey females (described in the text); *e, f, g, h*, double yellow females (described in text); *i*, non-disjunctional female of another origin (after Bridges), having three sex-chromosomes, shown for comparison. In all the figures are three pairs of autosomes. In the wild female (*a*) are two rod-shaped X-chromosomes (one from the father and one from the mother). In the triploid-X (*b, c, d*) and the double yellow (*e, f, g, h*) females is a single V-shaped body, the two attached X-chromosomes from the mother (sometimes with difficulty distinguishable from an autosome). In addition to these, there is: in the triploid-X females (*b, c, d*), a *rod-shaped* typical X-chromosome (derived from the father and accounting for the grey color of the fly); in the yellow females (*e, f, g, h*), the typical Y-chromosome (from the father). In the non-disjunctional female previously described by Bridges (*i*), the three sex-chromosomes are a Y-chromosome and two X-chromosomes not attached by their ends.

types there are the usual three pairs of autosomes, but the sex-chromosomes differ from the usual condition in that there is present in both types a U- or blunt V-shaped chromosome in place of a rod-shaped X-chromosome (Fig. 3, cf. *a* with *b, c, d* and *e, f, g, h*); this body is undoubtedly the united X's derived from the original mosaic. Besides the united X's from the mother, there is in the yellow female the typical hooked Y-chromosome, the sex-chromosome from the father (Fig. 3, *e, f, g, h*), and in the wild type female the chromosome from the father is the typical rod-shaped X (Fig. 3, *b, c, d*), whose presence gives her the wild type body color of her father. Thus the cytological evidence brings another confirmation of the chromosome theory of heredity.

Origin of the Mosaic.

The origin of the mosaic fly can be explained if at some division in the spermatogenesis of the father (perhaps at the equation division) the two halves of the X-chromosome failed to become completely detached, but remained fastened together at one of their ends, producing the V-shaped chromosome or double chromosome found in the germ cells of the female descendants. The sperm containing this chromosome must have fertilized an egg containing an X-chromosome with the differentials for forked and bar (this is known to have been the constitution of half of the eggs of the mother). An X-triploid fly was thus produced (cf. Fig. 2); the triploid condition remained, however, in only the anterior part of the fly, where the body color was wild type and the eyes were slightly bar. These characters, as stated, are as expected in an X-triploid, where two differentials for yellow are present with one for wild type, and one differential for bar with two for wild type. At an early stage the chromosome carrying forked and bar was eliminated, leaving part of the fly (the abdomen) with only two X-chromosomes, the attached yellow-bearing chromosomes (Fig. 2). The germ cells of the individual were derived from this part, and at the reduction division of the eggs there must have been extruded into the polar body (or remained in the egg) either the two attached X-chromosomes or no chromosome.

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